Palaeoenvironmental and sea level change

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Abstract
Ancient environmental and sea level changes are very likely to have played key roles in primate speciation, extinction, adaptation and dispersal. Most modern primates are ecologically dependent on trees and inhabit tropical environments, and the same was true for many extinct primates. In the warm Palaeocene and Eocene when the tropical broadleaf forest biome extended to high latitudes, primates inhabited North America and northern Eurasia. Ranges then contracted into lower latitudes in the Eocene and Oligocene when global cooling caused a commensurate reduction in suitable tree cover, only to expand again in the Miocene, when most primates across Africa, Eurasia and South America exploited diverse forest and woodland environments, which may have been very different to those observed in similar regions today. By the end of the Miocene through to the Pleistocene, grassland expansion allowed more terrestrial and open habitat primates to radiate, although most retained some ecological dependence on trees. Sea level changes occurring since the origin of primates, causing events such as the closure of the eastern Tethys Sea, appearance of the Isthmus of Panama, and shifts in south east Asian archipelagos, facilitated primate dispersal and diversification. Changes to ocean circulation caused by sea level change may have impacted global climate, which in turn would have altered primate environments.

Main Text
Ancient environmental and sea level changes are very likely to have played key roles in primate speciation, extinction, adaptation and dispersal. Most modern primates are ecologically dependent on trees and inhabit tropical environments, and the same was true for many extinct primates. Over the course of primate evolutionary history, their distributions have tracked changing global environments, from occupation of Europe and North America in the warm Palaeocene and Eocene when the tropical broadleaf forest biome extended to high latitudes, to contraction into much lower latitudes later on when global cooling caused a commensurate reduction in suitable tree cover. At regional and local levels, environmental changes create selective pressures that drive micro- and macroevolution and shape primate communities. Changing sea levels and the resulting presence or absence of landbridges between regions or continents also act in this way, as well as influencing dispersals. To understand primate evolution, therefore, we need to understand how sea levels, landmasses and environments have changed over time.

Palaeoenvironmental change
Environments have living (biotic) and non-living physical and chemical (abiotic) components. Biotic parts of the environment include bacteria, fungi, plants and animals, whereas abiotic components include temperature, rainfall, soil and rock type, light intensity, topography (land surface features),

presence or absence of water bodies, and natural disturbances such as fire. Although there are close links between climate and environment, climatic factors are not the only determinants of a given environment: two areas with very similar temperatures and rainfall, for example, might have very different vegetation because of underlying differences in soil composition and geology. The biotic and abiotic parts of ancient, or palaeo, environments can be discovered and reconstructed using evidence from the fossil and geological records. Although many past environments, habitats and ecological communities were very different to those in the present, and may not have modern analogues, a set of key principles and processes that are assumed to be constant over space and time provide a framework in which inferences about past environments can be made. This concept is known as 'uniformitarianism'. So, for example, although we cannot assume that an extinct species occupies the same environment as a closely-related modern species, it is possible to use our knowledge of adaptation in living organisms to identify morphological traits that correlate with particular functions and thus make inferences about the activities (and hence environments) of extinct individuals, on the basis that fundamental biomechanical principles have not altered over time.

Palaeoenvironmental reconstruction is complicated by the patchy nature of the fossil and geological records. There is no guarantee – and indeed it is highly unlikely – that all the plants and animals of an extinct community have been preserved in the fossil record. Similarly, sediments and rocks that record ancient environments may have been destroyed or obscured by more recent geological activity. When reconstructing ancient environments it is therefore important to take into account the processes leading (or not) to fossilisation and how those fossils then survive to be recovered. This forms part of the specialised field known as 'taphonomy'. Similar care must be taken when interpreting other parts of the geological record. Notwithstanding these caveats, a good deal is known about global, and in some cases regional and even local, palaeoenvironmental change since the origin of the primates.

Hypotheses of primate origins centre on arboreality. Then, as now, the radiation was linked to tropical forest environments. There is considerable debate over the group that represents the earliest primates, but a potential candidate is the arboreal Plesiadapiformes, present in the Palaeocene and Eocene of North America, Europe and Asia. Unequivocal primates the adapiforms and omomyids radiated in the Eocene and were also present in North America, Europe and Asia, where they too exploited arboreal niches. During the warm Palaeocene and Eocene, broadleaf forests were common in high latitudes far from the tropics, including the regions from which early primates (or primate-like mammals) have been recovered. The early Palaeocene plesiadapiform *Purgatorius* has tarsal (foot) bones with adaptations to arboreality and is found at a time when angiosperm (flowering) plants (which include broadleaf trees) were prevalent in the North American west (Chester et al. 2015). Detailed study of mammalian communities and fossil plants from north west Europe at the end of the Palaeocene and the beginning of the Eocene indicates the presence in Europe of warm-loving, dense, evergreen forest with a thick understory that gave way to forests with much less ground cover (Hooker and Collinson 2012). Interestingly, understory demise in this area is linked to incoming large browsing herbivores that fed on ground-living plants and created disturbance (Hooker and Collinson 2012) and is a good reminder that environmental change can be effected through a number of different means.

At a similar time, less dense, deciduous broadleaf forest characterised North American fossil regions such as the Bighorn Basin (Hooker and Collinson 2012). Thus, although a high latitude forest belt facilitating primate dispersal probably connected Asia, Europe and North America during the early Eocene (Smith et al. 2006), the structure of those forests may have varied in different places. Elsewhere in the world, angiosperms would also have provided habitat and food for primates. Although there is no lemur fossil record until the Pleistocene, meaning that taxa cannot be linked with particular environments, lemur ancestors probably arrived on Madagascar sometime in the Palaeocene or Eocene. Palaeoenvironmental modelling indicates that a diversity of biomes was present in Madagascar at this time, including moisture-loving forest in the centre and seasonal forests in the north west; there is no good evidence for spiny thicket (a characteristic habitat of modern southern Madagascar that supports several diverse species of lemur) until the Eocene-Oligocene boundary (Ohba et al. 2016).

As global climate cooled and thus became drier throughout the Eocene, environments in the northern hemisphere changed, with woodland (characterised, unlike forest, by having a grassy understory) and open environments replacing forests. The major extinction event at the end of the Eocene known as the Grand Coupure witnessed the loss of practically all European and north Asian primates and the vast majority of those from North America. Primate ranges contracted into those that are more familiar to us today, probably linked in part to the retreat of moist tropical forest biomes. The extensive primate fossil record from the Fayum (in modern day Egypt) provides an important window onto palaeoenvironments and adaptations during this period of transition. At the Fayum late Eocene Birket Qarun Locality 2 (BQ-2), from which adapiforms, stem and crown strepsirhines and anthropoids have been recovered as part of a diverse faunal record, study of primate morphological adaptations alongside data from study of fish fossils and sediments indicate forested habitats close to shallow freshwater streams or ponds that may have flooded seasonally, adjacent to the coast (Seiffert et al. 2008). Examination of palaeosols (fossil soils) from parts of the Oligocene Jebel Qatrani Formation also points to the presence of floodplain that contained standing water for some of the year (Bown et al. 1982). Fossilised wood and vegetation indicate tall trees and vines, and fossil root systems (rhizoliths) suggest the presence of mangroves (Bown et al. 1982). This is consistent with the arboreal adaptations evident in the postcrania of, for example, *Aegyptopithecus* (Bown et al. 1982).

Although very little is known about late Oligocene primates, emerging evidence from the Rukwa Rift in Tanzania, part of the East African Rift, is providing important clues to the palaeoenvironments of the earliest apes and Old World monkeys (Stevens et al. 2013). The Songwe member of the Nsungwe Formation has been reconstructed on the basis of sedimentary data to be semi-arid freshwater wetlands that contain aquatic and terrestrial animals (Roberts et al. 2010). At the Turkana Basin site of Lokone, from which a single primate has been recovered, sediments and fossil pollens suggest that humid woodlands and semi-deciduous forests surrounded a freshwater lake (Leakey et al. 2011). A handful of primates have been recovered from two other late Oligocene Turkana Basin sites, part of assemblages comprising mainly large terrestrial animals, with overall environments argued to be wooded and containing freshwater (Leakey et al. 2011).

By the late Oliogene and early Miocene, global temperatures had increased once more, and habitats suitable for primate exploitation became available at higher latitudes, including northern Eurasia and

southern South America. Neotropical primates are found in Patagonia and southern Argentina during the early and mid Miocene, where open temperate semi-arid forests and humid warm-temperate forests were found. The exceptional mid Miocene site of La Venta, Colombia, was unlikely to have contained continuous canopy evergreen forest of the type that characterises similar latitudes in South America today, instead having a varied environment comprising riverine forest and discontinuous canopy; large tusked herbivores may have helped shape the vegetation patterns (Kay and Madden 1997). The much more extensive primate fossil record of the Miocene, and large number of sites with associated palaeoenvironmental reconstructions, underlines the variation over time and in space that is possible in primate environments, even if trees are an important component. Evergreen, multi-canopied forest was probably present at the early Miocene African sites of Songhor and Mfwangano Island, but the rich floral assemblage from the Hiwegi Formation on Rusinga Island has been interpreted as single-canopied, disturbed woodland (reviewed in Elton 2008). A recent discovery in this formation of a fossil forest with *Proconsul* teeth closely associated in the same palaeosol, however, suggests widespread, dense, multistoried, closed-canopy forest that, when examined alongside other evidence from Rusinga, could underline the dynamic nature of the environment (Michel et al. 2014). African habitats in the mid Miocene may have been less variable, although environmental diversity is still evident. Fort Ternan, for example, is famous for grass flora but the apes including *Kenyapithecus* probably lived in seasonal woodland; *Kenyapithecus* is also found at Paşalar in Turkey, which probably had single-canopied, seasonal subtropical woodland or forest (reviewed in Elton, 2008). Woodland and freshwater environments probably characterised many monkey and ape sites in Eurasia and Africa in the late Miocene through to the early Pleistocene, when more extensive grassland and savanna habitats appeared, in response to the extreme cooling and drying trend that is a hallmark of the period. Some primates then began to exploit much more open environments. This is very clear, for example, in the southern African monkey assemblage of the Plio-Pleistocene, which is dominated by large, terrestrial species with origins that are tied to the expansion of grasslands (Elton 2007). Large, terrestrial or semi-terrestrial colobines also radiated at a similar time, and hominins evolved to exploit much more open habitats than other apes.

Many environments associated with hominins and monkeys in the Pliocene and Pleistocene are described as ‘mosaic’, comprising a mix of different habitat types that may include woodland, grassland and riverine or gallery forest. Such mixed environments are evident in many parts of the world and demonstrate that vegetation is highly responsive to localised conditions, such as the presence of rivers. Very few fossil plants are known from Plio-Pleistocene sites, and environmental reconstructions are often based the fauna recovered, interpreted in the context of other evidence such as climatic trends based on data from ocean cores and localised palaeosols. Taphonomic factors may mean that fauna are mixed from a number of different time periods and places (‘time and space averaging’), resulting in a ‘mosaic’ signal, which sometimes may not reflect the actual palaeoenvironment. However, it is possible to identify trends over time in a single region. At Plio-Pleistocene Koobi Fora in eastern Africa, for example, well-known for its extensive and diverse hominin and monkey fauna, analysis of the fauna show that environments changed from scrub woodland region with a flooding river, to open and riverine woodland with edaphic (poorly-drained or seasonally flooded) grassland, to drier grassland, and then to wetland and edaphic grassland (Reed 1997).

Sea level change

Sea level change can occur because of several different processes. For example, in the Pleistocene, sea levels fluctuated with global temperature, as the ice caps grew and therefore locked water into them, causing sea levels to lower in cold (glacial) periods, then partially melted during warmer periods, causing sea levels to rise. Warmer global temperatures also cause the sea to increase in volume and therefore increase sea levels. However, release of water is not the only process that occurs at the end of a glaciation. During glacial periods, the weight of the ice pushes the Earth's surface down, which 'bobs' back up when the ice melts and the pressure on the crust is relieved. This causes a landmass to rise, which may cause relative sea level to drop. Tectonic activity also alters sea levels, as plates move together and apart, changing the size of ocean basins or closing connections between seaways.

Rising sea levels that isolate land masses from one another promote diversification and ultimately speciation as gene flow between populations that were previously connected ceases (known as vicariance). Sea level changes in the Pliocene that periodically exposed and obliterated land bridges shaped dispersal and diversification of Sulawesi tarsiers (Driller et al. 2015), and later, responding to the immense sea level fluctuations caused by Pleistocene glacial cycles, also macaques. In fact, changes in sea level and associated shifts in the size and connections of landmasses are implicated in the dispersal and subsequent evolution of several groups of primates. Falling sea levels that expose landbridges allow taxa to disperse, shifting ranges and potentially creating competition in, and changes to, ecological communities joined by incomers. Towards the end of the early Miocene, tectonic plate movement caused the closure of the eastern end of the Tethys Sea (part of an ancient body of water, originally the Tethys Ocean separating the supercontinents of Gondwana and Laurasia), and connecting Eurasia and Africa. This allowed the dispersal from Africa first of apes, which then diversified rapidly and spectacularly in Eurasia in the mid Miocene, then, in the late Miocene, monkeys (which also underwent a radiation in Eurasia). Lowered sea levels between Africa and Arabia may have helped the spread of early guenons in the late Miocene (Gilbert et al. 2014) and baboons in the Pleistocene. The isolation of South America from North America (which occurred around 90 – 100 Ma) ended in the Pliocene. Although fossil evidence indicates that monkeys crossed a narrow seaway between the two continents in the early Miocene (Bloch et al. 2016), by at least 3.5 Ma the Isthmus of Panama (a physical land connection created either by tectonic activity or lowering of sea levels), allowed greater movement of primates into what is now Central America (Kay 2015), part of an extensive dispersal of mammals known as the Great American Interchange. Like other major seaway reconfigurations, the appearance of the landbridge between South and North America is likely to have changed ocean current circulation, which would have had an impact on global climate. This, in turn, would have influenced terrestrial environments, including those inhabited by primates.

See also: *Aegyptopithecus*, Adapiform; Angiosperm radiation theory; Biogeography and primate biogeography; Climate change and primate evolution; Evolution of the Cercopithecidae; Evolution of the Hominoidea; Evolution of modern strepsirrhines; Evolution of Neotropical primates; Hominins; Koobi Fora; Miocene primates; North American primate fossil record; Omomyid; Plate tectonics; Plesiadapiforms; Pleistocene primates; Pliocene primates; Primate origins: debates and controversies; *Purgatorius*.

References

Bloch JI, Woodruff ED, Wood AR, Rincon AF, Harrington AR, Morgan GS, Foster DA, Montes C, Jaramillo CA, Jud NA, Jones DS, MacFadden BJ. (2016) First North American fossil monkey and early Miocene tropical biotic interchange. Nature, DOI: 10.1038/nature17415

Bown, Thomas M., Mary J. Krause, Scott L. Wing, John G. Fleagle, Bruce H. Tiffney, Elwyn L. Simons, and Carl F. Vondra. 1982. "The Fayum primate forest revisted." *Journal of Human Evolution*, 11:603–632. doi:10.1016/S0047-2484(82)80008-0

Chester SGB, Bloch JI, Boyer DM, Clemens WA. 2015. Oldest known euarchontan tarsals and affinities of Paleocene *Purgatorius* to Primates *PNAS* 112: 1487-1492 doi:10.1073/pnas.1421707112.

Driller C, Merker S, Perwitasari-Farajallah D, Sinaga W, Anggraeni N, Zischler H. Stop and Go – Waves of Tarsier Dispersal Mirror the Genesis of Sulawesi Island. Janke A, ed. PLoS ONE. 2015;10(11):e0141212. doi:10.1371/journal.pone.0141212.

Gilbert CC, Bibi F, Hill A, Beech MJ (2014). Early guenon from the late Miocene Baynunah Formation, Abu Dhabi, with implications for cercopithecoid biogeography and evolution. PNAS 111: 10119-10124; doi:10.1073/pnas.1323888111

Elton, S. (2007). Environmental correlates of the cercopithecoid radiations. Folia Primatologica 78: 344-364.

Elton, S. (2008). The environmental context of human evolutionary history in Eurasia and Africa. Journal of Anatomy 212: 377-393.

Hooker JJ, Collinson ME 2014. Mammalian faunal turnover across the Palaeocene-Eocene boundary in NW Europe: the roles of displacement, community evolution and environment. Austrian Journal of Earth Sciences 105: 17-28.

Kay, R.F. 2015. Biogeography in deep time – What do phylogenetics, geology, and paleoclimate tell us about early platyrrhine evolution? Molecular Phylogenetics and Evolution 82: 358–374 doi:10.1016/j.ympev.2013.12.002

Kay RF, Madden RH. 1997. Mammals and rainfall: palaeoecology of the middle Miocene at La Venta (Colombia, South America). Journal of Human Evolution 32: 161 – 199.

Leakey, Meave, Grossman, Ari, Gutiérrez, Mercedes, Fleagle, John G. (2011). Faunal Change in the Turkana Basin during the Late Oligocene and Miocene. Evolutionary Anthropology 20: 238-253.

Ohba M, Samonds KE, LaFleur M, Ali JR, Godfrey LR 2016. Madagascar's climate at the K/P boundary and its impact on the island's biotic suite. Palaeogeography, Palaeoclimatology, Palaeoecology 441: 688-695; http://dx.doi.org/10.1016/j.palaeo.2015.10.028.

Michel LA, Peppe DJ, Lutz JA, Driese SG, Dunsworth HM, Harcourt-Smith WEH, Horner W, Lehmann T, Nightengale S, McNulty KP (2014). Remnants of an ancient forest provide ecological context for Early Miocene fossil apes. *Nature Communications* 5: 3236. doi: 10.1038/ncomms4236

Reed, K.E. 1997. Early Hominid Evolution and Ecological Change through the African Plio-Pleistocene. Journal of Human Evolution. 32, 289-322.

Roberts, Eric M., O'Connor, Patrick M., Stevens, Nancy J., Gottfried, Michael D., Jinnah, Zubair A., Ngasala, Sifael, Choh, Adeline M., and Armstrong, Richard A. (2010) Sedimentology and depositional environments of the Red Sandstone Group, Rukwa Rift Basin, southwestern Tanzania: new insight into Cretaceous and Paleogene terrestrial ecosystems and tectonics in sub-equatorial Africa. Journal of African Earth Sciences 57: 179-212.

Seiffert ER, Bown TM, Clyde WC, and Simons EL (2008) Geology, paleoenvironment, and age of Birket Qarun Locality 2 (BQ-2), Fayum Depression, Egypt. In Fleagle JG & Gilbert CC (eds) Elwyn L. Simons: A Search for Origins. New York: Springer, pp. 71-86.

Smith T, Rose KD, Gingerich PD (2006). Rapid Asia–Europe–North America geographic dispersal of earliest Eocene primate *Teilhardina* during the Paleocene–Eocene Thermal Maximum. PNAS 103: 11223-11227; doi:10.1073/pnas.0511296103

Stevens, Nancy J., Erik R. Seiffert, Patrick M. O'Connor, Eric M. Roberts, Mark D. Schmitz, Cornelia Krause, Eric Gorscak, Sifa Ngasala, Tobin L. Hieronymus, and Joseph Temu. 2013. "Palaeontological evidence for an Oligocene divergence between Old World monkeys and apes." *Nature*, 497:611–614. doi:10.1038/nature12161

Further reading

Bown, Thomas M., Mary J. Krause, Scott L. Wing, John G. Fleagle, Bruce H. Tiffney, Elwyn L. Simons, and Carl F. Vondra. 1982. "The Fayum primate forest revisted." *Journal of Human Evolution*, 11:603–632. doi:10.1016/S0047-2484(82)80008-0

Elton, S. (2008). The environmental context of human evolutionary history in Eurasia and Africa. Journal of Anatomy 212: 377-393.

Hooker JJ, Collinson ME 2014. Mammalian faunal turnover across the Palaeocene-Eocene boundary in NW Europe: the roles of displacement, community evolution and environment. Austrian Journal of Earth Sciences 105: 17-28.

Ohba M, Samonds KE, LaFleur M, Ali JR, Godfrey LR 2016. Madagascar's climate at the K/P boundary and its impact on the island's biotic suite. Palaeogeography, Palaeoclimatology, Palaeoecology 441: 688-695; http://dx.doi.org/10.1016/j.palaeo.2015.10.028.